HIBERNATION: A PERIODICAL PHENOMENON.

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Hibernation may be defined as the quiescent condition characteristic of many organisms during winter. A number of investigators have studied the phenomenon for the plant and animal kingdoms and have assembled a large mass of facts as to the physiological conditions and the habits of hibernating organisms. The studies have also included the causes of this quiescence and a number of hypotheses have been proposed.

Confining ourselves to insects the most commonly proposed hypothesis is that low temperature or low mean temperature is conducive to hibernation. In a previous paper[1] the author analysed an amount of temperature data with reference to the date of hibernation of the Codling Moth and showed that in the cases studied a marked lowering of average temperature or a very low temperature did not immediately precede the date of hibernation. The author has during the past two years carried on some experiments with the banana fly (*Drosophila melanogaster* Meigen) with the object of determining whether or not a hibernating period could be established by the stimulus of low temperatures. In this experiment eggs, larvæ, pupæ and adults of the same parents were kept in the ice box and in the greenhouse.

TABLE I.

Pupal Period.

Number Pupæ	Number Days in Ice Box	Temp.	Number Days in Greenhouse	Temp.
370	10	41-43° F.	8.43	58-86° F.
340	0	41-43° F.	9.09	58-86° F.

The proceedure was as follows: pupæ were placed in the ice box for ten days and then removed to the green house. At the date of removal pupæ which had just formed were also placed in the greenhouse. The periods of time that elapsed before emergence of the adults was then compared. The results show that a persistent quiescent condition was in no case brought about by this treatment. Larvæ and adults after twenty days in ice box were immediately activated by high temperature.

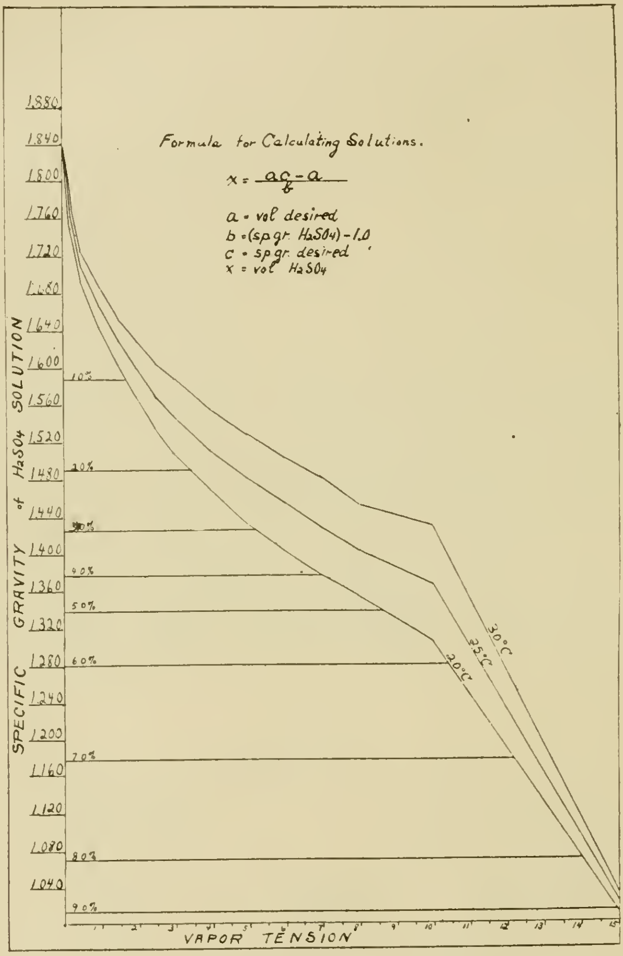

FIGURE 1

In order to avoid confusion it would be well to state, at this point, that in general hibernation in insects is characterized by quiescence which persists for sometime after the temperature has risen or continues through periods of high temperature. In many cases the phenomenon manifests itself before the temperature falls. In this case the condition can be recognized by a pause in feeding and in growth. The Codling Moth has already been cited as an example of this peculiarity. It might also be said that the food of the insect has not become less available at this period. Other common insects which hibernate as larvæ at a definite date irrespective of low temperatures are the Woolly Bear (Isia isabella) and an Arctiid (Apantesis nais). This "habit" was studied in 1915, especially with reference to its independence of stimulii from relative humidity.

The proceedure was as follows: Different relative humidities were maintained by solutions of H_2SO_4 of various sp. gr. as suggested by Woodworth[2] and which I calculated from figures given by Richards.[3] I have plotted the curve below from Richard's figures and used the formula accompanying it in the Volume calculations. (Figure 1).

The solutions (200 cc.) were placed in battery jars (capacity 2000 cc.) with broad ground edges, which were vasalened and covered with a glass plate. Inside these battery jars, supported over the H_2SO_4 by square glass dishes, were placed glass jars with a covering of cloth net in which the caterpillars were kept. Food was introduced daily into the jar and the sulphuric acid solution was changed every two weeks. The effects of different humidities was very apparent on the food introduced. In this work, due to the variation in temperature the humidity of any bottle also varied, but this change being equal in each bottle, the difference between bottles remained uniform. The moisture absorbed from food and insects by the H_2SO_4 is a source of error but not a great one.

The data derived from these experiments are shown in tables II and III.

TABLE II.

APANTESIS NAIS.

No. of Experiment..	9	11	12	13	14	15	16	17	27
Date..............	x/7	x/7	x/7	x/7	x/7	x/7	x/7	x/7	x/7
Number Specimens..	10	10	10	10	10	10	10	10	10
Vapor tention....... (15. = saturation)	9.	15.	5.6	13.5	11.	.5	13.8	.8	1.8
No. molted skins....	13	15	12	10	8	10	14	8	8
Date stopped feeding	x1/1	x1/4	x1/4	x1/29	x1/16	x/18	x1/4	x/16	x/16
Date of first death..	x1/1	x1/1	x/14	x11/2	x1/4	x/14	x/4	x/14	x/14
2nd Humidity...... (vapor tention)	13.8	5.6	15.	15.	15.	15.	5.6	15.	......
Date..............	x1/11	x1/11	x1/11	x11/4	x1/27	x/18	x1/11	x/18	......
Eating.............	......	......	......	......	......	x/18	......	x/18	......
Molts..............	......	......	......	......	......	1	......	1	......
Date Death.........	x1/20	x1/11	x1/16	......	......	x/21	x1/16	x/21	......
Date not Eating....	......	......	......	......	......	x1/27	......	x1/4	......

TABLE III.

III–38. Sixteen specimens of Isis isabella caterpillars.

DATE	VAPOR TENTION	BEHAVIOR
x1/20–x1/27	15.0	not eating, 1 molt.
x1/27–x1/29	9.0	" " 0 "
x1/29–x11/2	13.5	" " 0 "
x11/2–x11/7	15.	" " 0 "
x11/7–x11/9	13.8	" " 0 "
x11/9–x11/11	{13.8, 15.0}	" " 0 "
x11/11............	....	..............First Death.

Table III shows a great regularity in the date at which the caterpillars at the different humidities ceased feeding. This date can be considered as the beginning of hibernation, as no feeding took place later than this and all molting and metamorphosis ceased. Since these larvæ were exposed to a high temperature and had abundant fresh food present it is apparent that high temperature, abundant food and any relative humidity is not sufficient stimulus to overcome the "tendency" of the insects to hibernate. Table IV gives further support to this conclusion and also indicates that various successive treatments with different humidities are also of no avail. Death was not due to poisoning of the larvæ by fumes given off from H_2SO_4, for *Noctua unipuncta* moths were reared from first stage larvæ at vapor tentions 3.4, 9.0, 11., 13.5, 15.0.

Since larvæ before experiencing winter go into a hibernating condition from which various combinations of the three stimulii high temperature humidity and food cannot "arouse" them, we must conclude that this quiescence is predetermined. The practice of collectors and the experiments of Weissmann,[4] have shown that a period of low temperature makes it possible to activate hibernating insects by high temperature. Kirby and Spence[5] have suggested that this predetermination is instinctive as they observed that before winter insects suddenly at a definite date, independent of weather conditions, start an excited search for winter shelters. This "instinct" has probably been noticed by every collector of insects. However, this "instinct," if not directed by any external stimulus is rather hard to explain in cases where a summer and a winter generation occur.

Pictet[6] studied the *Lasiocampa quercus* and Dendrolimus larvæ which hibernate before the temperature has lowered. In the case of *Lasiocampa quercus*, the adult emerges in July, but larvæ appear in August and hibernate, beginning again to develop in Spring and pupating in June-July. By keeping the larvæ on ice it was possible to cause them to pupate in May. Continued selection of precocious larvæ for six generations decreased the length of larval life from 245 to 112 days. The pupal period was lengthened sufficiently to make up for the difference. Similar experiments with *Dendrolimus pini* gave a second generation and no persistence of the normal cycle. Pictet believes that this difference is due to the fact that *Lasciocampa quercus* feeds on the leaves of deciduous trees, while *Dendrolimus pini* feeds on the leaves of evergreen trees.

We have seen that certain insects have a definite periodical hibernation which is hereditary. This quiescence can only be overcome by a certain period of low temperature and the organisms then by a compensatory lengthening of the next stage regains its normal rhythm. Other insects are more plastic and instead of showing a definite period of hibernation, merely remain quiescent during periods of low temperature and are active immediately after the temperature is raised. Such insects can be reared all the year round in the greenhouse and may be exemplified by Drosophila, *Noctua unipuncta*, the cockroaches, *Musca domestica* and others. In fact, we have every degree of development of this periodicity.

The factors which have determined the variability of this characteristic may be seen from a survey of some insect life histories. These factors are of three kinds:

1. *Climate*.—As there is no cold period in the tropics, insects do not hibernate there. This lack of periodicity persists in insects introduced into the temperate regions. This is probably the case with Drosophila which cannot be induced to hibernate.
2. *Food*.—Insects which feed upon materials constantly available do not show a definite periodicity. Thus the house fly female will oviposit at any time of the year when the temperature is appropriate. Pictet has pointed out that insects which feed on evergreen trees are not as rhythmical in their hibernation as those which feed on deciduous trees.
3. *Exposures*.—The degree to which insects are each year exposed to the conditions of winter may also determine the elasticity of their periodicity. Thus the Woolly Bear, which hibernates under stones in rather an exposed condition, has a definitely established period of hibernation, whereas the Army Worm, which hibernates deep in the earth, is less exposed to the effects of winter and hence hibernates only upon direct stimulus.

These three factors may also determine the stage or stages in which different species of insects hibernate. The data on life histories contained in Judeich and Nitsche[7] are more available than any others, because the life cycles of different species are tabulated in a system of which I show a modification below. This method makes it possible to record scattered observations on different stages of the life cycle of an insect and finally to read the whole history at a glance. It would be a great advance if a repository for such data could be established at some university or other institution.

LEPIDOPTERA *Phycis tumidella* Zk.

Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
EEE	EEE	EEL	LLL	LLL	PPP	AAA	EEE	EEE	EEE	EEE	EEE

Dist.—Mid. Europe, S. France.
Larvæ—Skeletonize oak leaves, from one side only, working in a tunnel under roof of pcs. of leaves.
Pupæ—In cocoon under ground.
Judeich u. Nitsche, 1895, p. 1060.
Symbols A, E, L, P stands for adult, egg, larva and pupa respectively.

HYMENOPTERA *Lophyrus pini* L.

Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
ppp	ppp	ppP	AA EE PAA	*LLL*	*LLL*	PPA E	A E*LL*	*LLL*	*L*pp	ppp	ppp
ppp ppp	ppp ppp	ppP ppP	AA EE EE PAA EE PAA	LLL LLL 1 2'	LLL LLL	ppp PPA E	ppp A 2 ELL	ppp LLL	ppp Lpp	ppp ppp	ppp 1 ppp 2'

Symbols as above with addition of "p" for prepupa and numbers for alternating generations and *italicized* to indicate injurious period.

This method of tabulation is more easily read and used than the system sometimes employed by the U. S. Bureau in which a circle represents the whole year and different stages occupy sectors or are shown by spiral lines. In a life cycle that extended over several years, such a method would lead to endless complications.

For the Tortricids of European forests we find by compilation that those species which feed on the outside of the tree hibernate in a resistant stage that is, as eggs or pupæ—whereas those which feed on the inside (protected places) of the tree hibernate as larvæ.

TABLE IV.

SPECIES	FEEDING HABIT	HIBERNATING STAGE
Tortrix		
pinicolana Zll.	Outside on needles of Larch	Egg
murinana Hbn.	Outside on needles of White Fir	Egg
rufimitrana H.Sch.	Outside on needles of White Fir	Egg
viridana L.	Outside on leaves of Oak	Egg
buoliana Schiff.	Inside bud of Pine	Larva
nigricana H. Sch.	Inside bud of Fir	Larva
tedella Cl.	Inside needles of Pine	Larva
duplicana Zett.	Inside twigs of Pine	Larva
pactolana Zll.	Inside twigs of Pine	Larva
turionana Hbn.	Inside buds of Scotch Fir	Larva
strobilella L.	Inside cones of Pine	Larva
resinella L.	Inside bud *gall* of Pine	Larva, two years
zebeana Ratz.	Inside resinous gall of Larch	Larva, two years
duplana Hbn.	Outside on shoots of Fir	Pupa

Again compiling the data on the Noctuidæ from the same source similar results are obtained and it is also shown that food supply is a factor in the determination of the hibernating stage.

TABLE V.

Noctuidæ.

HIBERNATING STAGE					LARVAL FOOD HABIT
Any stage	Egg	Larva	Pupa	Imago	
1			1	2	Polyphagus
	3		4	1	Desciduous trees
			1		Evergreen trees
	1				Borer
		2			Underground

Compiled from life-histories of the following species:

Noctua satellitia L.
Noctua exolitia L.
Noctua piniperda Panz.
Noctua aprilina L.
Noctua ochracea Hbn.
Noctua segetum Schiff.
Noctua coryli L.
Noctua incerta Hfn.
Noctua vetusta Hbn.
Noctua pisi L.
Noctua gamma L.
Noctua trapezina L.
Noctua caeruleocephala L.
Noctua vestigealis Rott.
Noctua aceris L.
Noctua pulverulenta Esp.

In general, we may conclude that insects hibernate as (1) adults, when their food habits are such that oviposition can take place on the proper food at the earliest warm weather (2) as larvæ, when protected from the cold and thus able to continue feeding to the latest date possible, (3) as pupæ or eggs, because they are nonfeeding resistant stages.

There is no evidence available as to whether or not these adaptations were established by selection, mutation, or inheritance of acquired characters. The evidence does, however, show that hibernation has resulted from the repeated effect of winter upon the species and that the degree to which this phenomenon has become rhythmical has been determined by the habits of the insect.

LITERATURE CITED.

1. **Baumberger, J. P.** Ann. Ent. Soc. Amer., 7, 1914 (323-353).
2. **Woodworth, C. W.** Rept. College Agr. & Agr. Expt. St., Univ. Cal., June, 1914.
3. **Richards, T. W.** Proc. Amer. Ac. Arts & Sc., 33, 1897 (23-27).
4. **Weissmann, A.** "Essays on Heredity," 1889.
5. **Kirby, W.** and **Spence, W.** "An Introduction to Entomology," 3d Ed., Vol. II, 1823, London.
6. **Pictet, A.** IXe. Congr. Internat. Zool. Monaco, 1913 (774-778).
7. **Judeich, J. F.,** and **Nitsche, H.** "Lehrbuch der Mitteleuropaeischen Forstinsecktenkunde," Wein, 1895, Vol. I, II.